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Preliminary Phylogeny of *Halgerda* (Nudibranchia: Halgerdidae) from the Tropical Indo-Pacific, with Descriptions of Three New Species

by

Shireen J. Fahey and Terrence M. Gosliner
Department of Invertebrate Zoology and Geology, California Academy of Sciences
Golden Gate Park, San Francisco, California 94118

This paper discusses the systematics and phylogeny of the genus *Halgerda* from the tropical Indo-Pacific. Morphological and anatomical data from *Halgerda* species were used to construct a preliminary phylogeny. The phylogenetic analysis demonstrates the monophyly of *Halgerda* and its relationship to its outgroup *Asteronotus* Ehrenberg, 1831.

Two new species of *Halgerda* from Thailand are named and described anatomically. These two species, *Halgerda stricklandi* sp. nov. and *H. bacalusia* sp. nov., are highly derived in several aspects of their morphology. They appear to be sister species and are most closely related to *Halgerda aurantiomaculata* Allan, 1932. A third new species, *Halgerda diaphana* sp. nov., is the sister taxon to the three taxa named above.

Due to external morphological similarities, comparison of the three new species is made with the original descriptions of *Halgerda carlsoni*, Rudman 1978, *H. malesso* and *H. guahan* Carlson and Hoff, 1993, and *H. aurantiomaculata*. The coloration, reproductive system and the radular morphology of the new species differ significantly from *H. carlsoni* and the other previously described *Halgerda* species. Although the two new species from Thailand share some characteristics, they differ significantly in external and radular morphology. The new species from Okinawa, *Halgerda diaphana* shares some external characteristics with *H. aurantiomaculata* and *H. guahan*, but the reproductive morphologies differ significantly.

Fahey and Gosliner (1999) provided justification for placement of *Halgerda*, *Asteronotus*, *Aphelodoris*, and *Sclerodoris* in the Halgerdidae. Valdés and Gosliner (submitted) have shown that *Sclerodoris* is more closely related to other caryophyllidia-bearing dorids than to *Halgerda* and *Asteronotus*.

All twenty-two described species placed in *Halgerda* are found in the tropical Indo-Pacific, from South Africa as the western-most locality to the Hawaiian Islands in the east. Some of the species are known only from the original description and there is one undescribed *Halgerda* species that has been included in this analysis. That specimen is currently being studied.

This paper describes three new species of the genus, two from Thailand and one from Okinawa, based on material collected from these locations and deposited in the Department of Invertebrate Zoology of the California Academy of Sciences (CASIZ).

A preliminary analysis of the phylogeny of the genus *Halgerda* is presented for the first time, using one outgroup, *Asteronotus* to establish the polarity of the characters.

Species Description

Family Halgerdidae Odhner, 1926
Genus *Halgerda* Bergh, 1880
Type species: *Halgerda formosa* Bergh, 1880, by monotypy.

***Halgerda stricklandi* sp. nov.**
Figs. 1A, 2A, 3

Material Examined. — Holotype: CASIZ 115298, one specimen, dissected, Ko Ha, Thailand, Andaman Sea. 13 meters depth, November 1997. Collected and photographed by M. Strickland.

Distribution. — This animal is known only from Thailand, Andaman Sea (this study).

Etymology. — This animal is named for Mark Strickland who has kindly provided many slides and specimens of nudibranchs to the authors. His thoughtfulness and generosity are greatly appreciated.

Natural History. — The animal was found in the open on a rock wall.

External Morphology. — The preserved animal studied (CASIZ 115298) measured 35 mm. The body is firm and smooth, but rigid. The body profile is high and the dorsum has a series of orange-tipped, conical tubercles arranged in a reticulate pattern. There are larger, orange-tipped, conical tubercles at the junctions of the reticulate pattern. Just below the orange tips on the largest tubercles is a faint white ring. The ground color of the dorsum and foot is whitish with a gray tinge. There are small orange tubercles scattered thickly over the entire dorsum, extending down to the mantle margin. There are four midline points connecting this network. The oral tentacles are short and digitiform. The wide foot has an orange margin.

The long rhinophores are tapered towards the tips and angled posteriorly. The white translucent rhinophores have 17–19 transverse lamellae that are outlined in black on the anterior side. The rhinophores have yellow background coloration on the upper half. A vertical black line is present along the posterior face of the entire length of each rhinophore.

The gill has four branchial leaves that are pinnate. These leaves have black spots on the anterior side of the branches. Within the gill branches are numerous flattened, translucent structures that are glandular. The anal papilla is long and tubular with black coloration on both the posterior and anterior sides.

Buccal Armature. — The buccal mass is not pigmented. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radula (Fig. 3) of the holotype has a formula of 58 × 53.0.53 (CASIZ 115298). The middle lateral teeth are hamate (Fig. 3C). The five or so inner lateral teeth are smaller and have shorter hooks than the middle lateral teeth (Fig. 3B). The three outer lateral teeth are much smaller than the inner and middle lateral teeth and have blunt denticles (Fig. 3A).

Reproductive System. — The reproductive system is triaulic (Fig. 2A). The wide ampulla is elongate with a single curve. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The short vas deferens separates from the ampulla and widens into the large, greatly expanded portion of the glandular

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Figure 1. Living animals. A. *Halgerda stricklandi* sp. nov. (CASIZ 115298). Specimen, 35 mm, from Ko Ha, Thailand, Andaman Sea; 13 m depth, November 1997. Photo by M. Strickland. B. *Halgerda bacalusia* sp. nov. (CASIZ 115299). Specimen, 40 mm, from Richelieu Rock, Thailand, Andaman Sea; 28 m depth, November 1997. Photo by M. Strickland. C. *Halgerda diaphana* sp. nov. (CASIZ 070118). Specimen, 30 mm, from Okinawa, Ryukyu Islands, 2 km ENE southern tip; 23 m depth, March 1987. Photo by R. Bolland.

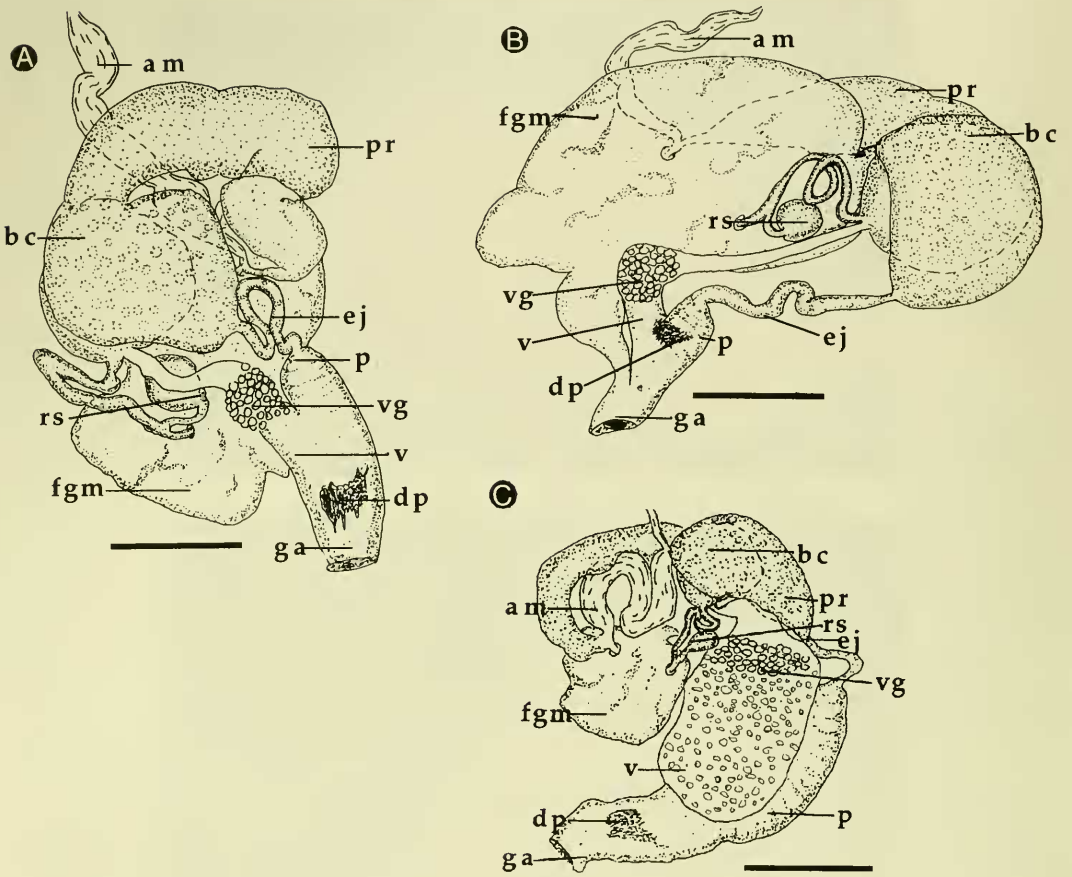

FIGURE 2. Reproductive systems. A. *Halgerda stricklandi* sp. nov. (CASIZ 115298; B. *Halgerda bacalusia* sp. nov. (CASIZ 115299); C. *Halgerda diaphana* sp. nov. (CASIZ 070118). Abbreviations: am = ampulla, bc = bursa copulatrix, dp = dark pigment, ej = ejaculatory duct, fgm = female gland mass, ga = genital atrium, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vg = vaginal gland. Scale bar = 1 mm.

prostate. The prostate consists of two distinct glandular types that are well differentiated, as is the prostate of most other members of *Halgerda*. The muscular portion of the vas deferens exits the prostate in a long, single convoluted duct, then widens sharply into the wide penial bulb. The female gland mass is about the same size as the prostate gland. The short uterine duct emerges from the female gland mass and joins the spherical receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is long and convoluted. The receptaculum seminis is smaller than the spherical bursa copulatrix. The large, thin-walled bursa is covered by the prostate. The vaginal duct that emerges from the base of the bursa copulatrix is long and thin. Near its exit adjacent to the base of the male aperture, is an enlarged, and obviously glandular portion of the vagina. The genital aperture is wide and large and the interior has dark pigmentation.

DISCUSSION. — *Halgerda stricklandi* has very similar external morphology to *H. malesso* Carlson and Hoff, 1993 and *H. carlsoni* Rudman, 1978. *Halgerda malesso* has the same smooth but firm, high body profile with angled tubercles tipped with orange, with orange spots scatted over the dorsum. In *H. malesso*, there is a network of orange lines between the ridges. At the juncture of the ridges are large, rounded tubercles with orange tips. Smaller orange-tipped tubercles are found along the ridge crests. The foot margin is orange.

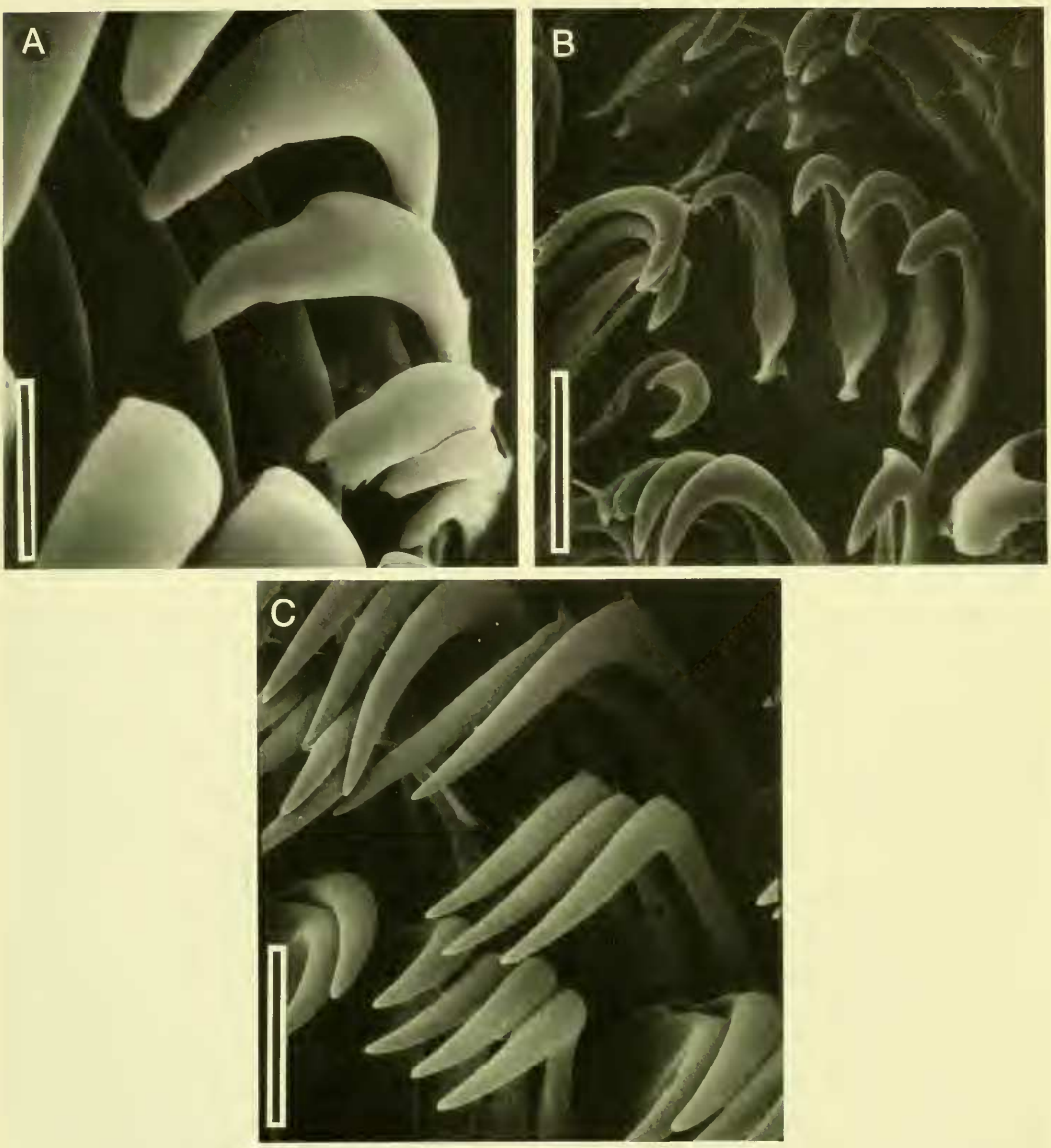

FIGURE 3. *Halgerda stricklandi* sp. nov. (CASIZ 115298). Scanning electron micrographs of radula. A. Outer lateral teeth, scale bar = 25 μm; B. Inner lateral teeth, scale bar = 43 μm; C. Middle lateral teeth, scale bar = 75 μm.

Halgerda carlsoni also has a high body profile with rounded tubercles tipped with orange or red as in the type specimen, *H. stricklandi*. There is an opaque white ring below each orange or red tip. Between the largest tubercles on the ridges are smaller orange or red-tipped tubercles. Scattered over the dorsum are numerous small orange or red spots. The foot margin has a band of orange or red. *Halgerda stricklandi* has the same orange-tipped tubercles as *H. malesso* and *H. carlsoni*, but they are more numerous. All three species have the same grayish white background color. *Halgerda stricklandi* differs from *H. malesso* and *H. carlsoni* in several other distinct ways:

1) The rhinophores of all three species are long and tapering, with the clavus angled posteriorly. The rhinophores of *H. stricklandi* have a yellowish club and black-edged lamellae with a black line on the posterior face. There is also a black line extending the length on the posterior side. *Halgerda malesso* and *H. carlsoni* have brown spots with brown lamellae and lack a line on the posterior side.

2) The four gill branchia of *H. stricklandi* are outlined with black on the posterior side, and there are black spots on the anterior side only. *Halgerda malesso* and *H. carlsoni* have brown spots around the branchia and they are not outlined in black.

3) All three species have a glandular portion of the vagina, but the vaginal duct of *H. malesso* is extremely wide compared to *H. stricklandi* and *H. carlsoni*. The vaginal ducts of *H. stricklandi* and *H. carlsoni* are similar and both are narrower than that of *H. malesso*.

4) The penis and the vagina are not joined basally into a common atrium in *H. malesso*, whereas in *H. stricklandi* and *H. carlsoni* they share a common opening. The penis in *H. malesso* is more bulbous than that of *H. stricklandi* and *H. carlsoni*, both of which have a more tubular penis that is larger than the vagina.

5) Both *H. malesso* and *H. stricklandi* have dark pigmentation on the genital atrium, however, the location of the pigmentation differs. In *H. malesso*, the pigmentation is at the top of the atrium, equidistant from both the vagina and penial openings. In *H. stricklandi*, the pigmentation lies in the penis, at the junction with the vagina. *Halgerda carlsoni* has no pigmentation.

6) The three outer lateral teeth of both species are smaller than the middle and inner lateral teeth. But all three outer teeth of *H. stricklandi* are denticulate whereas in *H. malesso*, only two are denticulate and the third is simple. Rudman (1978) reported the three outer teeth of *H. carlsoni* from Fiji as degenerate and not denticulate. However, specimens examined from Papua New Guinea had three denticulate outer teeth. In addition, *H. stricklandi* has very long, hamate, middle lateral teeth with much thinner hooks than those of *H. malesso* and *H. carlsoni*. Both *H. carlsoni* and *H. malesso* have very similarly-shaped inner and middle lateral teeth.

***Halgerda bacalusia* sp. nov.**
Figs. 1B, 2B, 4

MATERIAL EXAMINED. — HOLOTYPE: CASIZ 115299, one specimen, dissected, Richelieu Rock, Thailand, Andaman Sea. 28 meters depth, November 1997. Collected and photographed by M. Strickland.

DISTRIBUTION. — This animal is known only from Thailand, the Andaman Sea (this study) and from a photograph of a specimen from Mindanao, Philippines (M. Miller, pers. comm.).

ETYMOLOGY. — The trivial name *bacalusia* is Latin for a kind of confection or sweet, which this animal resembles with its bright, candylike colors.

NATURAL HISTORY. — This animal was found in the open on coral rubble substrate.

EXTERNAL MORPHOLOGY. — The preserved animal studied (CASIZ 115299) measured 40 mm. The body is firm and smooth, but rigid. The body profile is high and the dorsum has a series of orange ridges arranged in a reticulate pattern. There are four, orange-tipped, conical tubercles along the midline at the junctions of the ridges. Just below the orange tips on the largest tubercles is a faint yellow ring. The ground color of the dorsum and foot is whitish with a gray tinge. There are small orange dots scattered thickly over the entire dorsum, extending near, but not to the mantle margin. The small orange dots also terminate just below the orange coloration on the ridge crests. The white ground color is visible on the sides of the ridges. The mantle is lined with a bright yellow marginal band. The oral tentacles are short and digitiform. The wide foot has the same bright yellow margin as the mantle.

The long rhinophores are tapered towards the tips and angled posteriorly. They are translucent and have 17–19 transverse lamellae, which begin halfway up the stalk, which is ornamented with

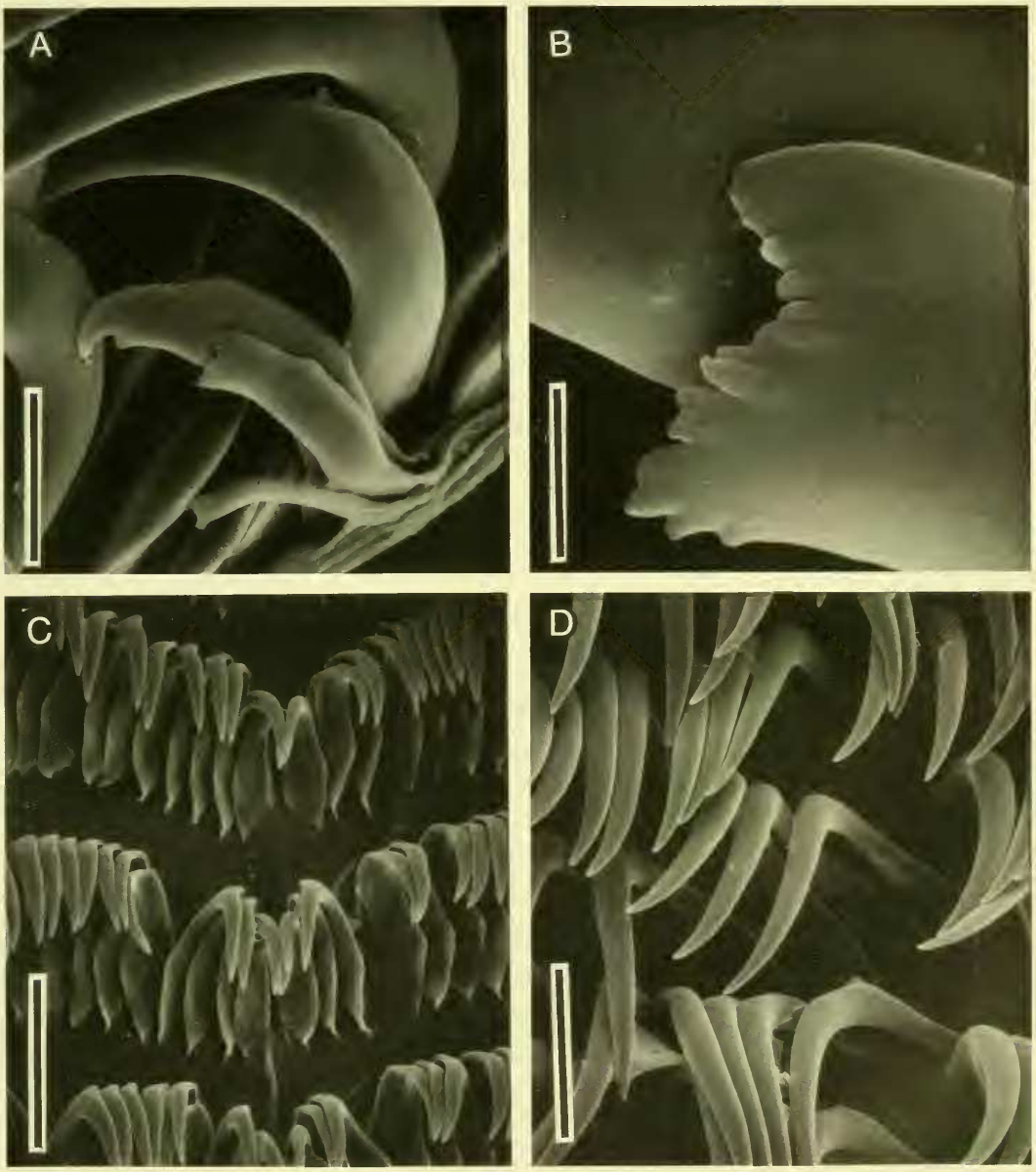

FIGURE 4. *Halgerda bacalusia* sp. nov. (CASIZ 115299). Scanning electron micrographs of radula. A. Outer lateral teeth, scale bar = 30 μm; B. Outer lateral teeth, scale bar = 4.3 μm; C. Inner lateral teeth, scale bar = 75 μm; D. Middle lateral teeth, scale bar = 100 μm.

black on the anterior side. The rhinophores have yellow background coloration on the upper half. A black longitudinal line is present on the posterior face and extends from the base to the club.

The gill has four branchial leaves that are highly pinnate. These leaves have black pigment on the margins and posterior sides of the branches. The tips of the branches are white. Within the gill branches are numerous flattened, translucent structures that are glandular.

BUCCAL ARMATURE. — The buccal mass is not pigmented. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radula (Fig. 4) of the holotype has a formula of 59 × 57.0.57 (CASIZ 115299). The middle lateral teeth are hamate, with long, thin hooks (Fig 4D). The inner lateral teeth are hamate, shorter than, and gradually increasing in size towards the middle of the half-row (Fig. 4C). The three outer lateral teeth are much smaller than the middle teeth and are not hooked but are denticulate (Fig. 4A, B). The denticles are blunt and numerous.

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Fig. 2B). The wide ampulla is elongate and flattened. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is longer than the prostate gland. The short vas deferens separates from the ampulla and widens into the large, widened portion of the glandular prostate. The prostate consists of two distinct glandular types and they are well differentiated as in most other members of *Halgerda*. The muscular portion of the vas deferens leaves the prostate in a long, single duct, then widens slightly into the penial bulb. The short uterine duct emerges from the female gland mass and joins the spherical receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is long and coiled. The spherical receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. The bursa is covered by the larger prostate. The vaginal duct that emerges from the base of the bursa copulatrix is long and thin. Near its exit adjacent to the base of the male aperture, is an enlarged and obviously glandular portion of the vagina. The genital atrium is wide and large and the interior has dark pigmentation.

DISCUSSION. — *Halgerda bacalusia* has very similar external and internal morphologies to *H. carlsoni* Rudman, *H. aurantiomaculata* Allan, and *H. guahan* Carlson and Hoff, but differs in several ways. Rudman (1978) described *H. carlsoni* from Fiji. The type specimen was described as having a smooth, ridged body, with a series of angled ridges. At the junctions of these ridges are red-tipped tubercles, which have a ring of white below the red tip. Between the largest tubercles on the ridges are smaller red-tipped tubercles. Scattered over the dorsum are numerous small red spots. The mantle margin is white with a border of orange or red spots. The foot has an orange-red border band.

Willan and Brodie (1989) recently redescribed *H. aurantiomaculata* (Allan, 1932) from Fiji. They described their two specimens as having a low body profile, with prominent pustules and a mid-dorsal ridge connecting the pustules. The pustules were capped with bright orange tips and the ridges had orange streaks along the summits. The mantle margin was orange and there were 3–8 orange spots of varying sizes in the depressions between the ridges. The foot had an orange margin.

Halgerda guahan Carlson and Hoff has the same firm, low body profile as *H. aurantiomaculata*. However, while it does have the characteristic ridges, it does not have pustules. The ridges are edged in yellow and the mantle margin and foot are edged in a thin, opaque white line.

Halgerda bacalusia also has a smooth, firm, high body profile with a series of angled orange ridges. There is also yellow coloration alongside the orange lines. At the junctions of these ridges are orange-tipped tubercles, which have a ring of yellow below the orange tip. Between the largest tubercles on the ridges are smaller, orange-tipped tubercles. Scattered over the dorsum are numerous small orange spots. The mantle has a bright yellow border, as does the foot.

In addition to the external coloration differences, *Halgerda bacalusia* differs from *H. carlsoni*, *H. aurantiomaculata* and *H. guahan* in the following ways:

1) All four species have long, tapering rhinophores. The rhinophores of both *H.carlsoni* and *H. bacalusia* have a yellowish club, and the edges of the lamellae have black pigment. The rhinophores of *H. aurantiomaculata* and *H. carlsoni* are covered with small, regularly-spaced, brown spots, which are darker on the stalk than on the club. The brown spots on the rhinophores are larger on *H. guahan* and the posterior side of the base has a thick brown streak on some specimens. *Halgerda bacalusia* has a black posterior line. The rhinophoral sheath of *H. guahan* also has a yellow margin. *Halgerda carlsoni* has 18-20 lamellae, all located near the tip, whereas *H. bacalusia* has 17–18 lamellae,

covering half the stalk and *H. aurantiomaculata* has 25 lamellae. The clavus of the rhinophores is angled posteriorly in all species.

2) The gill branches of *H. aurantiomaculata*, *H. guahan* and *H. carlsoni* have brown spots whereas *H. bacalusia* has dark pigment and no distinct spots.

3) There is a glandular portion of the vagina in *H. malesso*, *H. carlson*, *H. aurantiomaculata* and *H. bacalusia*. *Halgerda guahan* does not have this structure. The vaginal ducts of *H. bacalusia*, *H. guahan* and *H. carlsoni* are thinner than either *H. aurantiomaculata* or *H. malesso*. *Halgerda malesso* has a long, extremely wide vagina.

4) There is dark pigmentation on the genital atrium of *H. aurantiomaculata*, *H. malesso* and *H. bacalusia*, whereas *H. carlsoni* does not have this pigmentation. There is a common genital atrium in three species while in *H. guahan* the penis and vagina are separate to their distal ends.

5) The radular sac of *H. carlsoni*, *H. aurantiomaculata* and *H. bacalusia* is elongate. No information is available on the radular sac of *H. guahan* or *H. malesso*.

6) The three outer lateral teeth of *H. carlsoni* are much smaller than the middle lateral teeth. Although Rudman (1978) reported the three outer teeth as not denticulate, specimens examined from Papua New Guinea did have three denticulate outer teeth. The outer lateral teeth of *H. aurantiomaculata* are also smaller than the middle lateral teeth and sometimes weakly bifid (Willan and Brodie, 1989). Both *H. guahan* and *H. malesso* have three outer lateral teeth which are smaller than the middle teeth; two are denticulate and the third only slightly so. In all four species, the middle laterals are hamate.

Although *H. bacalusia* shares similar characters with *H. aurantiomaculata*, *H. carlsoni* and *H. guahan*, its unique combination of characters confirm it as a new species. The parsimony based analysis of the *Halgerda* genus also confirms that *H. bacalusia* is more closely related to *H. stricklandi* than to other members of the genus.

Halgerda bacalusia differs from *H. stricklandi* in the following ways:

1) External morphology. *Halgerda stricklandi* has orange-tipped conical tubercles, not connected by ridges. *Halgerda bacalusia* has orange and yellow-tipped tubercles connected by orange crested ridges. *Halgerda bacalusia* has a yellow-orange mantle margin and *H. stricklandi* has no coloration along the margin. The orange spots on the dorsum of *H. bacalusia* are tiny, whereas those of *H. stricklandi* are much larger and fewer.

2) Reproductive system. *Halgerda stricklandi* has a female gland mass approximately the same size as the prostate. *Halgerda bacalusia* has a female gland mass that is larger than the prostate. The ampulla of *H. stricklandi* is elongate with a single curve, and in *H. bacalusia*, the ampulla is elongate and flat. The dark pigmentation on the genital atrium of *H. stricklandi* is near the opening of the genital atrium, whereas the pigmentation on the genital atrium of *H. bacalusia* is near the juncture of the vagina and the penis.

3) Buccal armature. *Halgerda bacalusia* has blunt denticles on the three outer lateral teeth, and the denticles on *H. stricklandi* are sharper. The inner teeth of *H. stricklandi* are hamate with short hooks and those of *H. bacalusia* are hamate with long hooks.

***Halgerda diaphana* sp. nov.**

Figs. 1C, 2C, 5, 6, 7

MATERIAL EXAMINED. — HOLOTYPE: CASIZ 079369, one specimen, 34 mm. 1 km WNW Onna Village, Horseshoe Cliffs, Ryukyu Islands, Okinawa. 50 meters depth, September, 1991. Collected by R. Bolland. PARATYPES: CASIZ 070118, one specimen, 30 mm, dissected. 2 km ENE southern tip, Ryukyu Islands, Okinawa. 23 meters depth, March, 1987. Collected and photographed by R. Bolland. CASIZ 074688, one specimen, 25 mm. 1 km WNW Onna Village, Horseshoe Cliffs, Ryukyu Islands, Okinawa. 60 meters depth, March, 1984. Collected by R. Bolland. CASIZ 079368, one specimen, dissected, 39 mm. 1 km WNW Onna Village, Horseshoe Cliffs, Ryukyu Islands, Okinawa. 27 meters depth, August, 1991. Collected by R. Bolland. CASIZ 084877, one

specimen, 49 mm. Seragaki Beach, 1.3 km ENE of Maeki-zaki, Ryukyu Islands, Okinawa. 47 meters depth, October, 1991. Collected by R. Bolland. CASIZ 086598, one specimen, 37 mm. Seragaki Beach, 1.3 km ENE of Maeki-zaki, Ryukyu Islands, Okinawa. 3 meters depth, May, 1992. Collected by R. Bolland. CASIZ 087900, one specimen, 69 mm. Seragaki Beach, 1.3 km ENE of Maeki-zaki, Ryukyu Islands, Okinawa. 43 meters depth. August, 1992. Collected by R. Bolland. CASIZ 089002, one specimen, 49 mm. 1.3 km ENE of Maeki-zaki, Seragaki Beach, Ryukyu Islands, Okinawa. 3 meters depth. September, 1992. Collected by R. Bolland. CASIZ 089012, one specimen, dissected, 50 mm. 1 km WNW Onna Village, Horseshoe Cliffs, Ryukyu Islands, Okinawa. 55 meters depth, December, 1992. Collected by R. Bolland. CASIZ 104698, one specimen, 29 mm. 1 km WNW Onna Village, Horseshoe Cliffs, Ryukyu Islands, Okinawa. 30 meters depth. November, 1994. Collected by R. Bolland. CASIZ 105305, one specimen, dissected, 53 mm. Seragaki Tombs, Ryukyu Islands, Okinawa. 25 meters depth. November, 1994. Collected by R. Bolland.

DISTRIBUTION. — This animal is known only from the Ryukyu Islands, Okinawa (this study).

ETYMOLOGY. — The trivial name *diaphana* is from the Greek word *diaphanes* meaning a gauzy texture that is translucent or transparent, like the dorsum of this new species.

NATURAL HISTORY. — This animal is found from 3–60 meters depth, on various substrates from rock and coral rubble to silty sand. It has also been found on vertical rock walls and on the reef forefront on coral rubble and in crevices at the reef edge.

EXTERNAL MORPHOLOGY. — The preserved animals dissected (CASIZ 070118, 079368 and 105305) are 30 mm, 25 mm, and 30 mm respectively, in length. The body is firm and smooth, but rigid. Although the body profile is slightly arched, this species does not have the high body form common in most other *Halgerda*. The dorsum has orange crested ridges arranged in a distinct triangular pattern of three points per side of the dorsum. There are four pustules at the centerline of the dorsum that join the orange crests. There are secondary orange lines in the concavities of the ridges. The ground color of the dorsum and foot is translucent white, with the viscera clearly visible through the dorsum. The mantle submargin is lined in bright orange, and some animals have yellow coloration on the outside of the orange margin. The mantle edge is bright white. The oral tentacles are short and digitiform. The wide foot has the same bright orange submargin as the mantle.

The long rhinophores are tapered towards the tips and the bulb is angled posteriorly. The white translucent rhinophores have 18 transverse lamellae, which begin halfway up the stalk. The rhinophores have black speckles sprinkled liberally along their length. The extreme tip of the rhinophore is white.

There are two main branchial leaves that are moderately pinnate. Each of the two main leaves divides into three branches, with the posterior two being more pinnate than the anterior pair. The gills have the same black speckles that completely cover the rhinophores. The extreme tip of each branchia is white. Within the gill rachis are numerous flattened, translucent structures that are glandular. The anal papilla is long and tubular with black speckles on both the posterior and anterior sides.

BUCCAL ARMATURE. — The buccal mass is not pigmented. The radular sac is elongate and protrudes well behind the posterior end of the buccal mass. The radular formulae of the dissected specimens are $53 \times 43.0.43$ (CASIZ 070118), $49 \times 50.0.50$ (CASIZ 079368) and $55 \times 51.0.51$ (CASIZ 105305). The outer and middle lateral teeth are hamate (Figs. 5, 6, 7). The 10 innermost lateral teeth are hamate and small, then significantly larger towards the middle of the half-row (Figs. 5, 6, 7). The three outer lateral teeth are much smaller than the middle teeth and are not hooked but some are denticulate (Figs. 5, 6, 7). The denticles are blunt and numerous.

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Fig. 2C). The wide tubular ampulla is elongate and lies tightly against the female gland mass. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is about the same size as the prostate gland. The short vas deferens separates from the ampulla and widens into the large glandular prostate. The prostate consists of two distinct glandular types, which are well differentiated as in most other members of *Halgerda*.

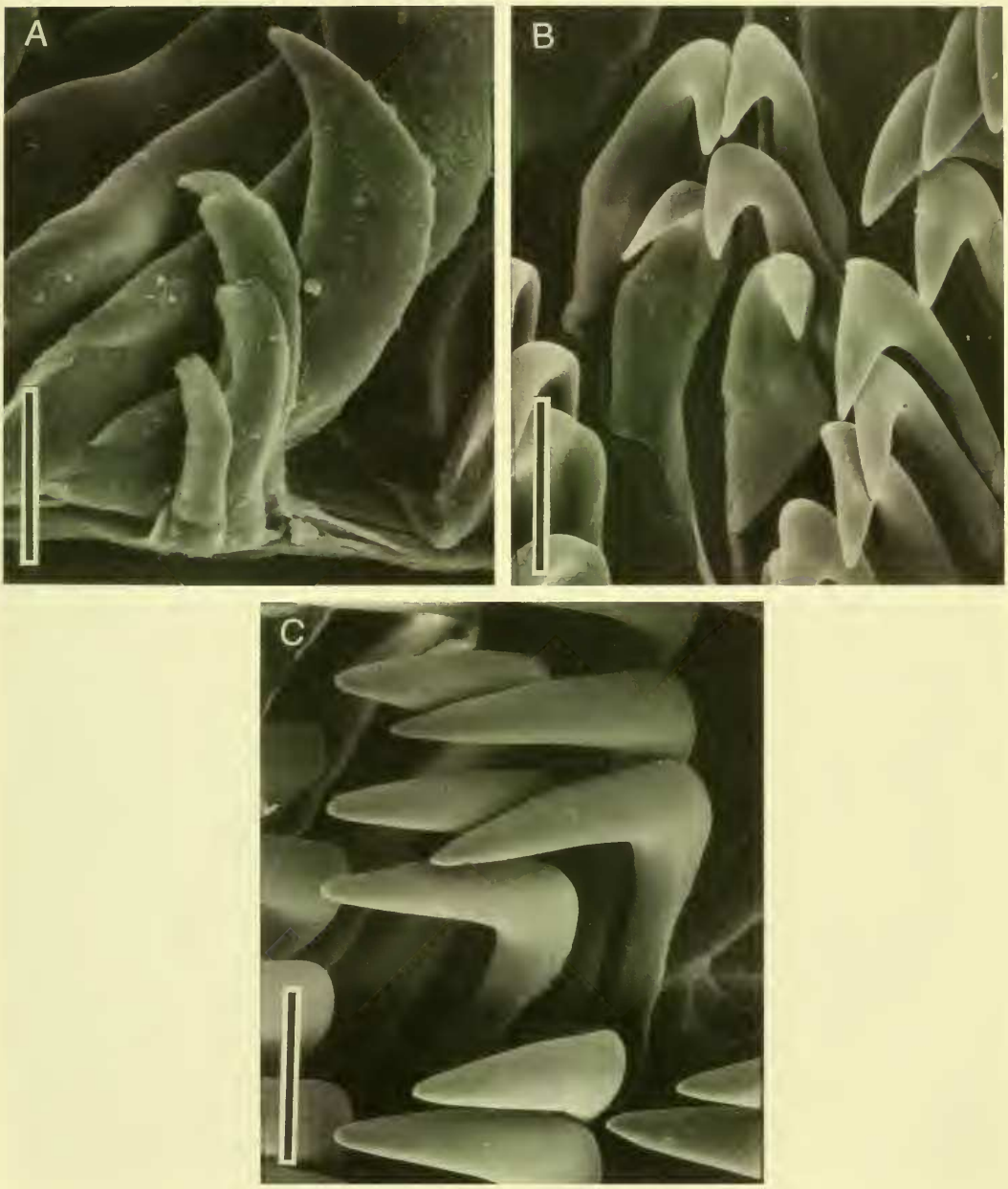

FIGURE 5. *Halgerda diaphana* sp. nov. (CASIZ 070118). Scanning electron micrographs of radula. A. Outer lateral teeth, scale bar = 25 μm; B. Inner lateral teeth, scale bar = 25 μm; C. Middle lateral teeth, scale bar = 60 μm.

The vas deferens leaves the prostate in a long, single duct, then widens substantially into the long, muscular portion of the penial bulb. The short uterine duct emerges from the female gland mass and joins the pyriform receptaculum seminis at its base. The duct connecting the receptaculum and the bursa is moderately long and convoluted. The pyriform receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. The bursa is covered by the larger prostate. The vaginal

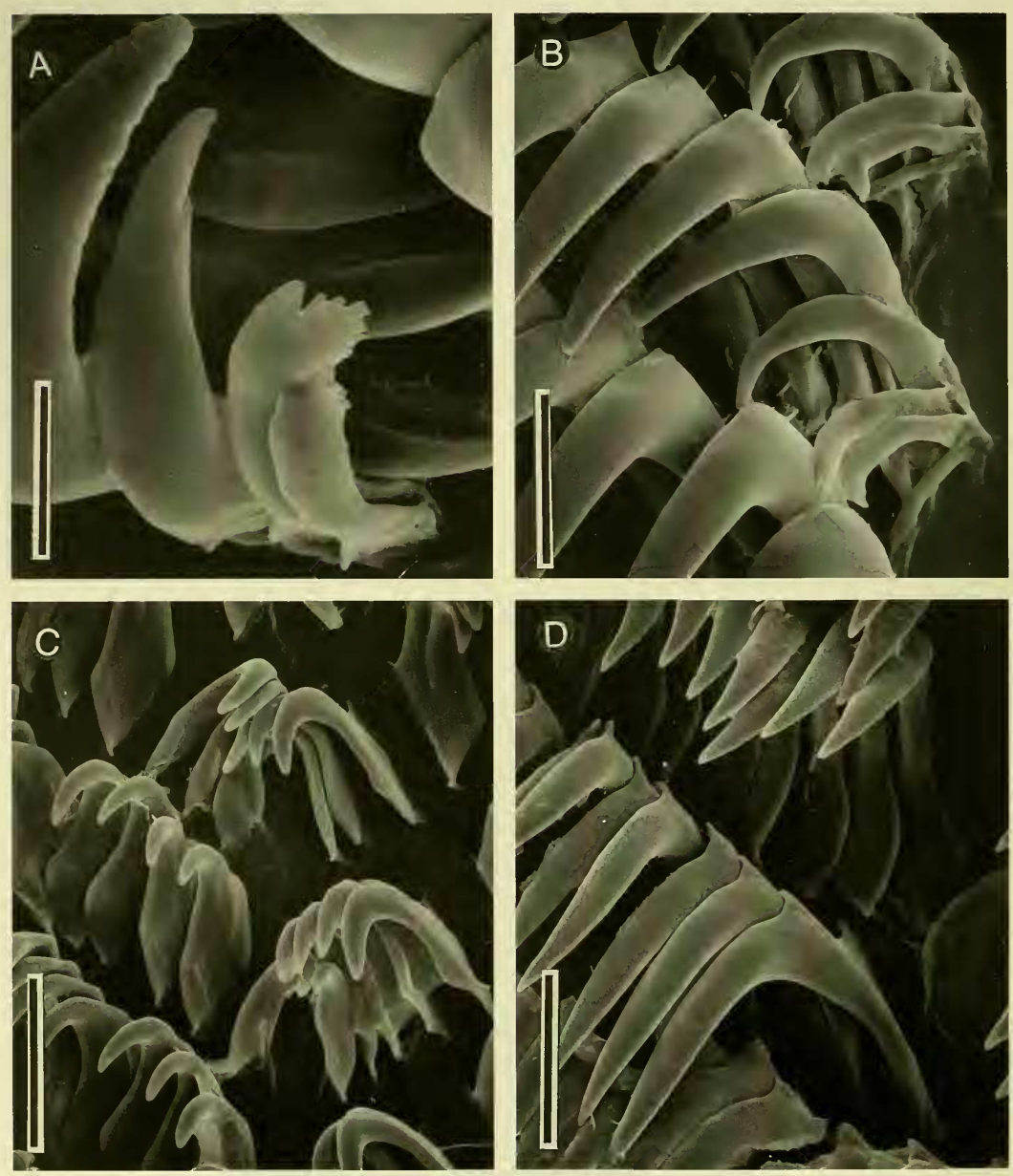

FIGURE 6. *Halgerda diaphana* sp. nov. (CASIZ 079368). Scanning electron micrographs of radula. A. Outer lateral teeth, scale bar = 15 μm. B. Outer lateral teeth, scale bar = 43 μm. C. Inner lateral teeth, scale bar = 43 μm. D. Middle lateral teeth, scale bar = 60 μm.

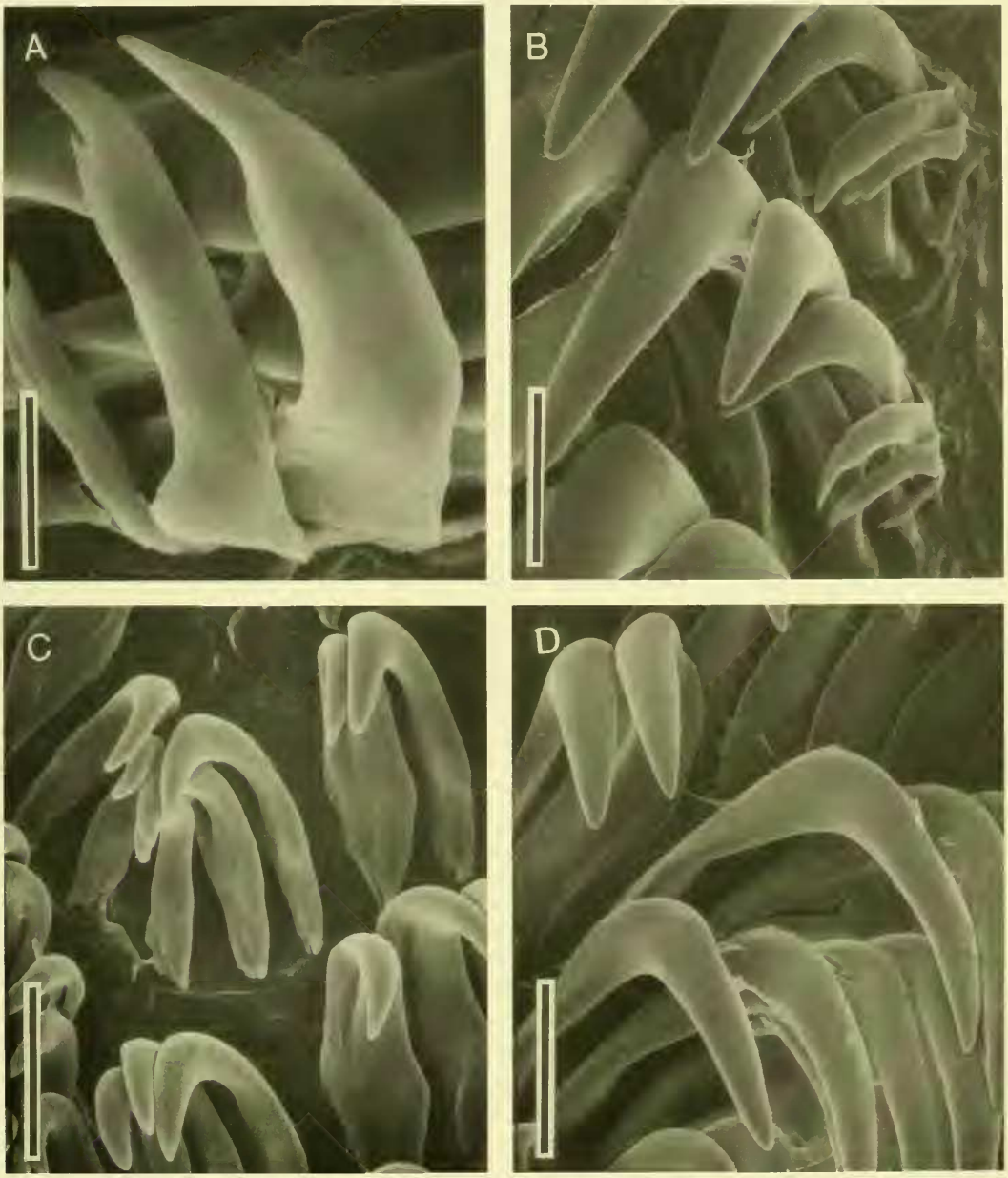

FIGURE 7. *Halgerda diaphana* sp. nov. (CASIZ 105305). Scanning electron micrographs of radula. A. Outer lateral teeth, scale bar = 15 μm; B. Outer lateral teeth, scale bar = 60 μm; C. Inner lateral teeth, scale bar = 43 μm; D. Middle lateral teeth, scale bar = 100 μm.

duct that emerges from the base of the bursa copulatrix is short and immediately widens into the very large and glandular vagina. The openings of the vagina and the penis share the common genital atrium, which has dark pigmentation half-way down its length on the interior of the duct.

DISCUSSION. — *Halgerda diaphana* shares similar external characteristics with *H. aurantiomaculata* and *H. guahan*. Carlson and Hoff (1993) described *H. guahan* from Guam and Willan and Brodie (1989) redescribed *H. aurantiomaculata* from Fiji. *Halgerda guahan* and *H. aurantiomaculata* have the same firm, low body profile as *H. diaphana*. However, while *H. guahan* has the characteristic ridges, it does not have pustules. *Halgerda aurantiomaculata* has prominent pustules, with four along the midline of the dorsum like *H. diaphana*. The ridges of *Halgerda guahan* are edged in yellow and the mantle margin and foot are edged in a thin, opaque white line. *Halgerda diaphana* and *H. aurantiomaculata* both have orange ridge crests and orange coloration submarginally along the mantle margin. The orange submarginal band on the mantle of *H. diaphana* is edged in bright white whereas the mantle margin of *H. aurantiomaculata* is orange. *Halgerda aurantiomaculata* has orange spots of various sizes on the mantle in the ridge concavities, while *H. diaphana* has secondary orange lines in the concavities.

There are several other distinct differences between *H. diaphana*, *H. aurantiomaculata* and *H. guahan*:

1) The rhinophores of both *H. diaphana* and *H. aurantiomaculata* have black speckles along the entire length. *Halgerda guahan* has brown spots on the rhinophores which are larger and the posterior side of the base has a thick brown streak on some specimens. The rhinophoral sheath of *H. guahan* also has a yellow margin. The club of the rhinophores is tilted backwards in all three species.

2) There is a glandular portion of the vagina in *H. aurantiomaculata*, whereas the entire vagina of *H. diaphana* is glandular. *Halgerda guahan* does not have this glandular structure. The vaginal duct of *H. guahan* is longer and thinner than that of either *H. aurantiomaculata* or *H. diaphana*.

3) There is dark pigmentation on the genital atrium of both *H. aurantiomaculata* and *H. diaphana* whereas *H. guahan* does not have this pigmentation (C. Carlson, pers. comm.). There is a common genital atrium in *H. aurantiomaculata* and *H. diaphana* while in *H. guahan* the penis and vagina are separate.

4) The outer lateral teeth of *H. diaphana* are much smaller than the middle lateral teeth, and are denticulate. The outer lateral teeth of *H. aurantiomaculata* are also smaller than the middle lateral teeth and sometimes weakly bifid (Willan and Brodie 1989). *Halgerda guahan* has three outer lateral teeth which are smaller than the middle teeth; two are denticulate and the third only slightly so. In all three species, the middle laterals are hamate.

Although *H. diaphana* shares similar characters with *H. aurantiomaculata* and *H. guahan*, its unique combination of characters establishes it as a new species. The parsimony based analysis of the *Halgerda* genus confirms that *H. diaphana* is a sister taxon to *H. aurantiomaculata*, *H. bacalusia*, and *H. stricklandi* and is more closely related to them than to other members of the genus.

PHYLOGENETIC RELATIONSHIPS

Phylogeny of *Halgerda*

Species of *Halgerda* have been recently described by several authors (Rudman 1978; Bertsch and Johnson 1982; Willan and Brodie 1989; Carlson and Hoff 1993; Yonow 1993; Gosliner and Fahey 1998; and Fahey and Gosliner, 1999). Additional data were taken from the original publications on *Halgerda* (Bergh 1880; Eliot 1904; Farran 1905). Valdés and Gosliner's data (submitted) were used for the character description of *Asteronotus*. In addition, the following species were examined directly: *Halgerda formosa* Bergh, 1880; *H. elegans* Bergh, 1905; *H. albocristata* Gosliner and Fahey, 1998; *H. willeyi* Eliot, 1904; *H. dalanghita* Fahey and Gosliner, 1999; *H. bacalusia* Fahey and Gosliner, 1999; *H. carlsoni* Rudman, 1978; *H. tessellata* Bergh, 1880; *H. stricklandi* Fahey and

Gosliner, 1999; *H. dichromis* Fahey and Gosliner, 1999; *H. toliara* Fahey and Gosliner, 1999; *H. terramtuentis* Bertsch and Johnson, 1982; *H.* sp. 2, undescribed species.

Thus, previous literature and direct observation and dissection of 13 species of *Halgerda* and members of the outgroup have provided the information on the characters for the present study of the phylogenetic relationships of *Halgerda* species. To establish the polarity of the morphological characters (Table 1) used in this study, one outgroup was selected based on a review of anatomical characters. We used *Asteronotus* as the outgroup rather than *Sclerodoris*, based on the phylogenetic study of Valdés and Gosliner (submitted).

The following characters were considered in this analysis:

[Note: Characters in parentheses were deleted from the first analysis, because they are phylogenetically uninformative. Those character descriptions preceded by an asterisk were deleted from a second analysis that tested how color characters (and phylogenetically uninformative characters) affect the tree topology.]

1. *Rhinophores.—All species of *Halgerda* have elongate rhinophores. The outgroup taxon, *Asteronotus* has short rhinophores and this character is considered plesiomorphic.

2. *Ridges.—All *Halgerda* have dorsal ridges. These ridges can be low-lying and almost level with the rest of the notum or they can be quite high and distinct. *Asteronotus* does not have ridges. The absence of ridges is considered the pleisiomorphic state.

3. Tubercles.—Rounded dorsal tubercles are absent in seven *Halgerda* species. Distinct rounded tubercles are present on nine *Halgerda* species, while pointed tubercles are present on another seven species. *Asteronotus* has prominent rounded tubercles, which are connected in concentric circles. The absence of tubercles is considered pleisiomorphic.

4. Small marginal tubercles.—Small tubercles are found along the mantle edge of four species of *Halgerda*: *H. brunneomaculata*, *H. formosa*, *H. tessellata*, and *H. toliara*. The outgroup taxon, *Asteronotus* does not have these marginal tubercles, and their presence is considered apomorphic.

5. *(Caryophyllidia.—No species of *Halgerda* or *Asteronotus* have caryophyllidia. This character is not applicable to the taxa being studied since caryophyllidia are absent from the outgroup and ingroup taxa studied).

6. *Body color.—The plesiomorphic state of an orange-yellow or reddish body color is shared by the outgroup taxon and four *Halgerda* species: *H. brunneomaculata*, *H. xishaensis*, *H. dalanghita*, and *H. toliara*. All other *Halgerda* have a white to gray-white background color.

7. Ridge color.—Three *Halgerda* have white dorsal ridges: *H. albocristata*, *H. xishaensis*, *H. dalanghita*. All others have orange or yellow ridges, while the outgroup taxon has the same coloration over its entire dorsum. Ridges that are the same color as the dorsum are considered the plesiomorphic state.

8. *Dark marginal lines.—Black marginal lines are unique to four *Halgerda*: *H. albocristata*, *H. elegans*, *H. iota*, and *H. willeyi*. The marginal lines lie perpendicular to the mantle edge. These marginal lines are not present on the outgroup taxon. Lack of marginal lines is the plesiomorphic state.

9. *Dark spots.—Black dorsal spots are present on four *Halgerda*: *H. brunneomaculata*, *H. formosa*, *H. punctata*, and *H. dichromis*. These spots can range from deep purple-black to dark brown. The outgroup taxon does not have these distinguishing spots, and this state is plesiomorphic.

10. Gill branching.—Only two *Halgerda* species share the tripinnate gill branching pattern with the outgroup taxon. Those two are *H. xishaensis* and *H. dalanghita*. The tripinnate gill pattern is considered plesiomorphic.

11. *Gill spots.—Dark spots on the gill branches are considered the apomorphic state. Nine species have these symmetrical round spots. Fourteen *Halgerda* species lack spots and share the plesiomorphic state with the outgroup taxon.

TABLE 1. Characters and states considered for the phylogeny of *Halgerda*.

	Character	Plesiomorphic	Apomorphic
1	Rhinophores	0 = short	1 = elongate
2	Ridges	0 = absent	1 = present
3	Tubercles	0 = absent	1 = rounded, 2 = pointed
4	Small marginal tubercles	0 = absent	1 = present
5	Caryophyllidia	0 = present	1 = absent
6	Body color	0 = reddish or orange	1 = whitish
7	Ridge color	0 = body color	1 = orange/yellow, 2 = white
8	Dark marginal lines	0 = absent	1 = present
9	Dark spots	0 = absent	1 = present
10	Gill branching	0 = tripinnate	1 = bipinnate
11	Gill spots	0 = absent	1 = present
12	Gill stripes	0 = absent	1 = present
13	Gill tip color	0 = white	1 = black
14	Gill shape	0 = erect	1 = flat
15	Gill pinnation	0 = highly pinnate	1 = moderately, 2 = sparsely pinnate
16	Rhinophore base color	0 = same as body color	1 = dark blotches, 2 = dark spots 3 = dark stripes
17	Rhinophore bulb color	0 = white	1 = black
18	Gill glands	0 = same as gill color	1 = opaque white
19	Oral tentacles shape	0 = short and rounded	1 = long and tapered
20	Foot border color	0 = absent	1 = present
21	Foot lines	0 = absent	1 = present
22	Foot spots	0 = absent	1 = present
23	Body shape	0 = broad	1 = elongate
24	Secondary orange lines	0 = absent	1 = present
25	Orange dots on dorsum	0 = absent	1 = present
26	Radula sac shape	0 = short	1 = elongate
27	Buccal mass	0 = unpigmented	1 = pigmented
28	Radula shape	0 = square	1 = rectangular
29	Middle lateral teeth	0 = hamate	1 = elongate
30	Outer lateral teeth shape	0 = hamate	1 = fimbriate
31	Outer lateral teeth size	0 = same size as middle laterals	1 = smaller than middle laterals
32	Fimbriate tooth length	0 = short	1 = long
33	Ampulla length	0 = short	1 = long
34	Vaginal duct length	0 = short	1 = elongate
35	Vaginal duct shape	0 = narrow	1 = wide
36	Vagina duct termination	0 = enters common atrium	1 = separate duct
37	Vaginal base shape	0 = narrow	1 = wide
38	Vaginal sphincter	0 = absent	1 = present
39	Prostate	0 = one part	1 = two parts
40	Differentiation of prostate	0 = poorly differentiated	1 = well differentiated
41	Ejaculatory duct	0 = short	1 = elongate
42	Receptaculum seminis	0 = same size as bursa copulatrix	1 = smaller than bursa
43	Tubercular vaginal glands	0 = absent	1 = present
44	Penis shape	0 = tubular	1 = bulbous
45	Uterine duct insertion	0 = base of bursa	1 = more distal
46	Prostate size	0 = smaller than female gland mass	1 = equal to female gland mass
47	Atrium pigment	0 = absent	1 = present
48	Mantle margin	0 = absent	1 = orange/yellow, 2 = white

12. Gill stripes.—Lack of dark gill stripes is the plesiomorphic state, and twelve species share this state with the outgroup. Ten species have dark stripes on the gill branches. The stripes run from bottom to top, along the posterior of the gill rachis.

13. *Gill tips.—All but five *Halgerda* species share the plesiomorphic character with the outgroup taxon with white gill tips that are the same color as the rest of the gill. The five *Halgerda* species that have black gill tips are: *H. albocristata*, *H. elegans*, *H. formosa*, *H. iota*, and *H. toliara*.

14. Gill shape.—Only two *Halgerda* species have gill branchia which lie flat on the dorsum: *H. punctata* and *H. dichromis*. All other species including the outgroup taxon have erect gill branchia. This is considered the plesiomorphic state.

15. Gill pinnation.—The plesiomorphic character state is a highly pinnate gill. This state is shared by the outgroup taxon and *H. dalanghita*. All other *Halgerda* have a moderately pinnate gill except for *H. brunneomaculata* and *H. toliara* which have a sparsely pinnate gill.

16. *Rhinophore base.—The rhinophoral base is the same as the body color in *Asteronotus*. Three *Halgerda* species share this plesiomorphic character state: *H. albocristata*, *H. elegans*, and *H. toliara*. The three other character states: dark blotches, dark spots and dark stripes are distributed among the other *Halgerda* species. This character is treated as unordered.

17. Rhinophore bulb.—A rhinophoral bulb that is the same color as the body is the plesiomorphic state, and only *Asteronotus* has this character state. All *Halgerda* species have dark coloration on the bulb.

18. (Gill glands.—All *Halgerda* share the apomorphic character state of opaque white glands internal to the gills. This character state could not be determined for *H. xishaensis*. The outgroup taxon has gill glands which are not opaque.)

19. (Oral tentacles.—Short rounded oral tentacles are plesiomorphic. Half of the *Halgerda* species share this character state with the outgroup taxon. The character state could not be determined from the literature for *H. iota*).

20. Foot border.—*Asteronotus* does not have a colored margin around the foot. Nine *Halgerda* species have a yellow or orange foot margin. This character state could not be determined for *H. dichromis*. Lack of a foot margin is considered plesiomorphic.

21. *Foot lines.—Dark-colored foot lines are absent in the outgroup taxa, and in most *Halgerda* species. However, *H. iota*, *H. tessellata*, and *H. willeyi* have dark lines along the edge of the foot. The presence of dark lines on the foot is considered apomorphic.

22. *Foot spots.—Over half of the *Halgerda* species have dark spots on the foot. *Asteronotus* and the other half of the *Halgerda* species do not have dark foot spots. This is considered the plesiomorphic state.

23. *Body shape.—*Asteronotus* has a broad body shape, the plesiomorphic state. This shape is shared by half the *Halgerda* species. The other half have a more elongate body shape.

24. *Secondary orange lines.—Ten *Halgerda* species have secondary orange lines on the notum between the ridges. *Asteronotus* does not have these secondary lines, and this is considered the plesiomorphic state.

25. *Orange dots.—Orange dots on the notum is the apomorphic character state of five *Halgerda* species: *H. aurantiomaculata*, *H. carlsoni*, *H. punctata*, *H. stricklandi*, and *H. bacalusia*. The outgroup taxon and the remaining *Halgerda* do not have orange dots on the notum.

26. Radular sac.—The radular sac of most *Halgerda* is elongate. Only *H. dalanghita* has a short radular sac, which is the plesiomorphic character state of the outgroup taxon *Asteronotus*. This character state could not be determined for five taxa.

27. *Buccal mass.—Most *Halgerda* species have an unpigmented buccal mass as does *Asteronotus*. However, *H. albocristata*, *H. formosa*, *H. wasinensis*, and *H. willeyi* all have dark pigmentation on the buccal mass. An unpigmented buccal mass is the plesiomorphic state. This character state could not be determined for *H. graphica*, *H. xishaensis* or *H. dichromis*.

28. Radula shape.—The shape of the radular ribbon is nearly square in *Asteronotus* and *H. dalanghita*. This radula shape is the plesiomorphic state. All other *Halgerda* species have a rectangular radular ribbon.

29. Middle lateral teeth.—All *Halgerda* species except *H. dalanghita* share the plesiomorphic character state of hamate middle lateral teeth. *Halgerda dalanghita* has elongate, middle lateral teeth.

30. Outer lateral teeth shape.—Pointed, undivided outer lateral teeth is the plesiomorphic character state which is shared by *Asteronotus*, *H. graphica*, *H. iota*, *H. willeyi*, and *H. dalanghita*. The remaining *Halgerda* species have fimbriate outer lateral teeth.

31. Outer lateral teeth size.—Only *H. dalanghita* has outer lateral teeth that are the same size as the middle lateral teeth. *Asteronotus* and all other *Halgerda* species have smaller outer lateral teeth than the middle teeth. The presence of smaller outer lateral teeth is the plesiomorphic state.

32. Fimbriate teeth.—Of the species which have fimbriate outer teeth, only *H. albocristata*, *H. brunneomaculata*, and *H. elegans* have elongate fimbriate teeth. All other species have short fimbriate teeth. The presence of short, fimbriate, outer lateral teeth is considered the plesiomorphic character state. This character state is not relevant for five species, including the outgroup (see character 30 above).

33. Ampulla length.—A short ampulla is considered plesiomorphic. This character state is shared by both the outgroup taxon and five *Halgerda* species. All other *Halgerda* have a long ampulla. Data were unavailable for four species: *H. graphica*, *H. iota*, *H. punctata*, and *H. xishaensis*.

34. Vagina length—Six *Halgerda* species share the plesiomorphic character state of a short vagina with *Asteronotus*. All other *Halgerda* have an elongate vagina. Data were unavailable for the same four species as in character 33.

35. Vagina shape.—The outgroup taxon and nine *Halgerda* species have a narrow vagina. The other *Halgerda*, for which data were available, have a wide vagina. A narrow vagina is the plesiomorphic character state.

36. Vagina duct.—The vaginal duct enters the common atrium proximally in the outgroup taxon and in all *Halgerda* except *H. albocristata*, *H. aurantiomaculata*, *H. elegans*, and *H. guahan* in which they are separate to the base. Data were unavailable for the same four species noted above. A common atrium is the plesiomorphic state.

37. Vaginal base.—A narrow vaginal base is considered the pleisiomorphic character state. All *Halgerda* share this state with the outgroup taxon except *H. formosa*, *H. tessellata*, *H. wasinensis*, *H. willeyi*, and *H. diaphana*. No data are available for the four *Halgerda* species mentioned previously.

38. Vaginal sphincter.—A sphincter at the top of the vagina is present in five *Halgerda* species: *H. formosa*, *H. tesselata*, *H. wasinensis*, *H. willeyi*, and *H. dichromis*. No sphincter is present in the outgroup taxon, and this is considered the pleisiomorphic state. No data are available for the same four *Halgerda* species as above.

39. (Prostate.— All *Halgerda* and *Asteronotus* have a two-part prostate. Data were unavailable for the same four species as noted above).

40. (Differentiation of prostate.—All taxa studied except *H. dalanghita* have a well-differentiated prostate. A well-differentiated prostate is the apomorphic state. Data were missing for the same four species noted above).

41. Ejaculatory duct.—A short ejaculatory duct is the plesiomorphic character state, and the outgroup taxon shares this state with eight *Halgerda* species. The ejaculatory duct is elongate in all other *Halgerda* for which data were available.

42. Receptaculum seminis.—The receptaculum seminis is about the same size as the bursa copulatrix in the outgroup taxon, in *H. brunneomaculata* and *H. carlsoni*. In all other *Halgerda* for which data were available, the receptaculum is smaller than the bursa.

43. Tubercular vaginal glands.—Tubercular vaginal glands are present in eight *Halgerda* species. This is considered apomorphic. Lack of tubercular vaginal glands is the character state shared by the outgroup taxon and the remaining *Halgerda* species for which data were available.

44. Penis.—Four *Halgerda* species have a tubular penis. All other *Halgerda* for which data were available have a bulbous penis like *Asteronotus*. A bulbous penis is the plesiomorphic state.

45. Uterine duct insertion.—The uterine duct inserts at the base of the bursa in the outgroup taxon, and in half the *Halgerda* species. In the other *Halgerda* species, the duct inserts at a point more distal to the bursa, closer to the receptaculum seminis. This is considered apomorphic. No data were available for the same four *Halgerda* species.

46. (Prostate.—The prostate is smaller than the female gland mass in the outgroup taxon and in half the *Halgerda* species. In the other half, the prostate is the same size as the female gland mass. The smaller prostate is considered plesiomorphic. No data were available for the same four species as above).

47. *Atrium pigment.—Dark pigmentation is present on the genital atrium of six *Halgerda* species. All other species, including the outgroup taxon have no pigmentation on the genital atrium. This is the plesiomorphic state.

48. Mantle margin.—A colored margin around the perimeter of the mantle is a character state shared by six *Halgerda* species. The outgroup taxon does not have a colored mantle margin. Lack of a colored mantle margin is considered pleisiomorphic.

Methods

In order to develop phylogenetic hypotheses regarding *Halgerda*, the above described characters were placed into a data matrix (Table 2) from MacClade version 3.04 (Maddison and Maddison 1998). All characters used have equal weight and are unordered. Six characters were deleted from the first analysis due to being parsimoniously uninformative. The characters deleted are indicated in parentheses in the character descriptions (previous section). The data were analyzed by Phylogenetic Analysis Using Parsimony (PAUP) version 4.0b2 by David Swofford (1999). A heuristic search was performed with the optimality criterion of maximum parsimony. The stepwise addition option of Random Trees was used, with 100 repetitions, starting from random start trees. Four most parsimonious trees were produced. The trees required 128 steps and had a consistency index of 0.375. The strict consensus tree is shown in Figure 8. Figure 9 shows the majority rule tree with the character numbers and character reversals. The underlined numbers indicate reversals.

An evaluation was performed of one million trees sampled randomly from the set of all possible trees. The mean of that evaluation is 205.2, the standard deviation is 7.72, the g1 statistic is –0.34 and the g2 statistic is 0.08.

A decay analysis was performed using a heuristic search by PAUP for all trees ≤129 steps. The stepwise addition option of Random Trees was used, with 100 repetitions, starting from random start trees. A 50% majority-rule consensus of 390 trees was computed. The Consistency Index (CI) is 0.372 for this tree.

A second analysis was performed deleting color-based characters to determine the impact of these characters on the tree topology. An asterisk preceding the character description (previous section) indicates the characters deleted for this analysis. The data were analyzed by the same method using PAUP as described for the first analysis. Figure 10 shows the strict consensus of 72 most parsimonious trees obtained by deletion of the color characters. The tree required 77 steps and had a CI of 0.42.

Discussion

Character analysis indicated that nearly half of the characters were subject to at least one instance of homoplasy, either parallelism or reversal. Figure 9 shows those characters by number. Some of these characters are: small marginal tubercles; elongate, fimbriate outer teeth; a long ampulla; a wide

TABLE 2. Data Matrix. Character states in species of *Halgerda* and the outgroup *Asteronotus*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
H. albocristata	1	1	2	0	1	1	2	1	0	1	0	0	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	1	0	1	1	1	1	0	0	1	0	0	1	1	1	1	0	1	1	1	0	0
H. aurantiomaculata	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	0	1	0	0	0	0	1	1	0	1	0	1	1	0	1	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1
H. brunneomaculata	1	1	0	1	1	0	1	0	1	1	0	1	0	0	2	3	1	1	1	0	0	1	1	0	0	?	0	1	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
H. carlsoni	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	0	1	0	0	0	0	1	1	0	1	0	1	1	0	1	1	1	0	0	0	1	1	1	0	1	1	1	0	0	0
H. elegans	1	1	2	0	1	1	1	1	0	1	0	0	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	1	0	1	1	1	1	1	0	1	0	0	1	1	1	1	0	0	1	0	0	0
H. formosa	1	1	0	1	1	1	1	0	1	1	0	0	1	0	1	1	1	1	1	1	0	1	1	0	0	1	1	1	0	1	1	0	1	1	1	0	1	1	1	1	0	1	0	1	1	1	0	0
H. graphica	1	1	2	0	1	1	1	0	0	1	0	1	0	0	1	3	1	1	0	0	0	0	0	1	0	?	?	1	0	0	1	?	?	?	?	?	?	?	1	?	?	1	?	?	?	0	?	0
H. guahan	1	1	0	0	1	1	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	1	1	1	0	1	0	1	0	1	1	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	0	0
H. iota	1	1	2	0	1	1	1	1	0	1	0	0	1	0	1	3	1	1	?	0	1	1	0	0	0	?	0	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
H. malesso	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	0	1	0	0	0	1	0	?	0	1	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	1	0	1	1
H. punctata	1	1	1	0	1	1	1	0	1	1	0	1	0	1	1	3	1	1	0	0	0	1	1	0	1	1	0	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
H. terramtuentis	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	1	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	1	1	1	1	1	1	0	0	0	0
H. tessellata	1	1	2	1	1	1	1	0	0	1	0	1	0	0	1	3	1	1	1	0	1	1	1	1	0	1	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	1	0	1	0	1
H. wasinensis	1	1	2	0	1	1	1	0	0	1	0	1	0	0	1	1	1	1	1	0	0	1	1	1	0	1	1	1	0	1	1	0	1	0	0	0	1	1	1	1	0	1	0	1	0	1	0	0
H. willeyi	1	1	0	0	1	1	1	1	0	1	0	1	0	0	1	3	1	1	1	0	1	1	0	0	0	1	1	1	0	0	1	?	0	1	0	0	1	1	1	1	0	1	0	1	0	1	0	0
H. xishaensis	1	1	0	0	1	0	2	0	0	0	1	0	0	0	1	2	1	?	0	0	0	0	0	0	0	?	?	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
H. dalanghita	1	1	2	0	1	0	2	0	0	0	0	1	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	0	?	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
H. sp. 2	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	0	1	0	0	0	1	0	1	0	1	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	0
H. stricklandi	1	1	1	0	1	1	1	0	0	1	1	1	0	0	1	3	1	1	1	1	0	0	0	0	1	1	0	1	0	1	1	0	1	1	1	0	0	0	1	1	0	1	1	1	0	0	1	0
H. bacalusia	1	1	1	0	1	1	1	0	0	1	0	1	0	0	1	3	1	1	0	1	0	0	0	0	1	1	0	1	0	1	1	0	1	1	1	0	0	0	1	1	0	1	1	1	0	0	1	1
H. dichromis	1	1	0	0	1	1	1	0	1	1	0	1	0	1	1	1	1	1	1	?	?	?	1	0	0	1	?	1	0	1	1	0	0	1	0	0	0	1	1	1	1	1	0	1	0	1	0	0
H. toliara	1	1	0	1	1	0	1	0	0	1	0	0	1	0	2	0	1	1	1	0	0	0	1	1	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	2
H. diaphana	1	1	1	1	1	1	1	0	0	1	1	0	0	0	1	2	1	1	0	1	0	0	1	1	0	1	0	1	0	?	1	?	1	0	1	0	1	0	1	0	0	1	1	1	0	1	1	1
Asteronotus	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

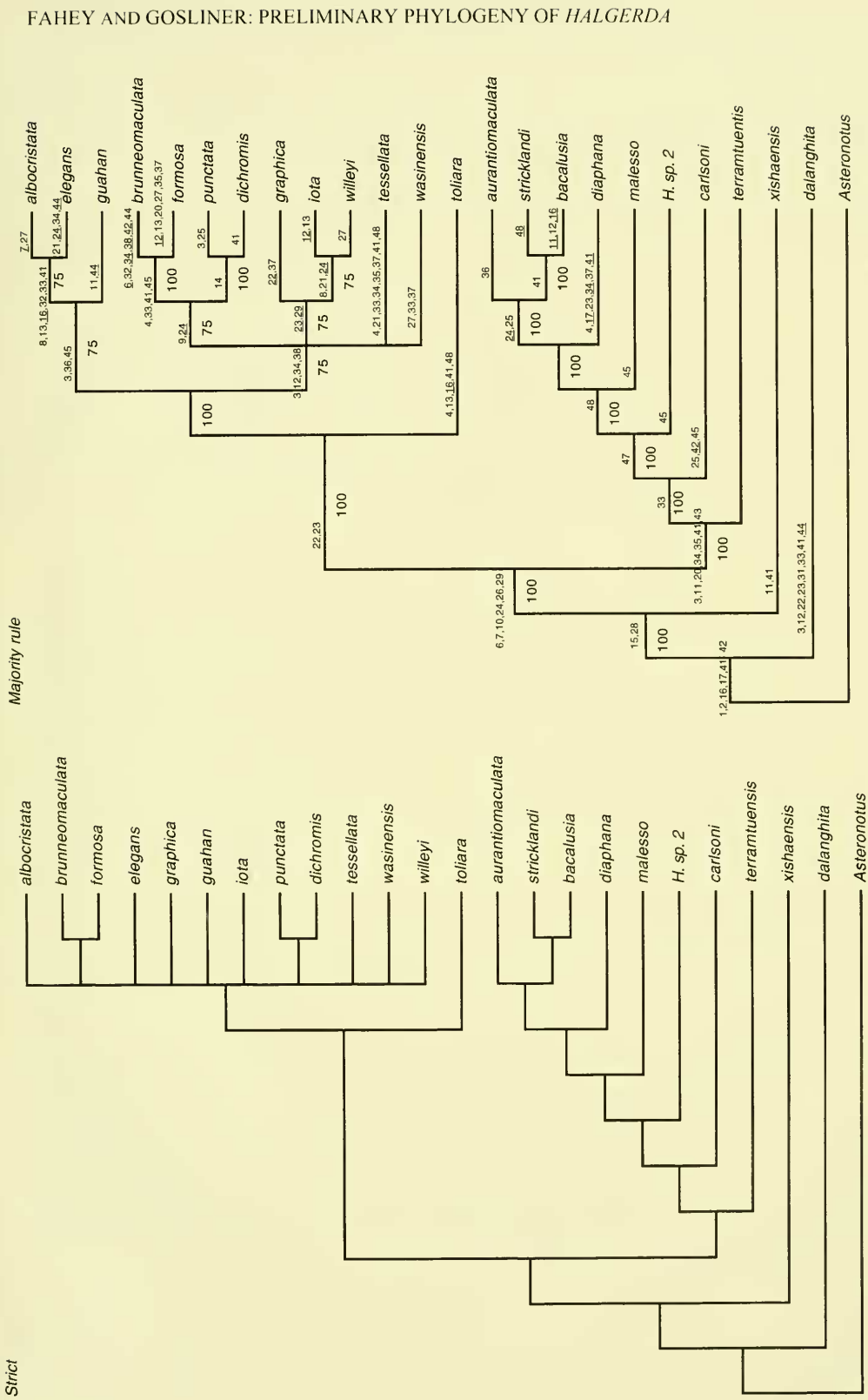

FIGURE 8. Preliminary Phylogeny of *Halgerda*. Strict consensus of four most parsimonious trees. *Asteronotus* was chosen as the outgroup to polarize the characters.

FIGURE 9. Majority rule tree of four most parsimonious trees showing character tracings. Numbers below the branches refer to percentage of trees supporting the branch. Numbers above the branches refer to character numbers shown in Table 1. Underlined numbers indicate reversals.

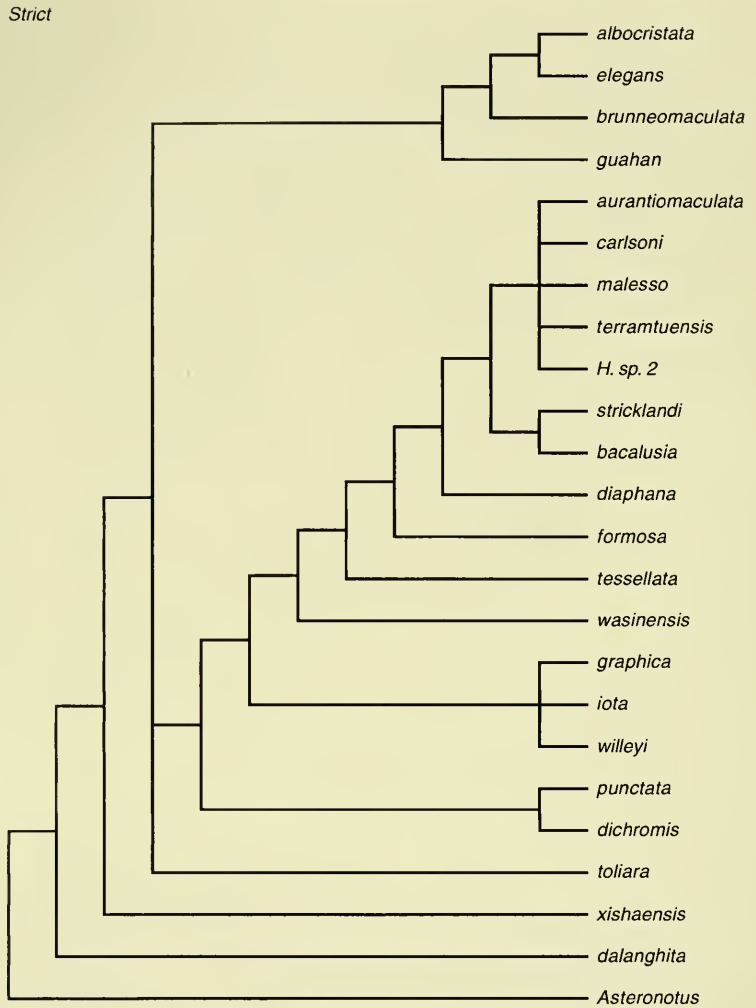

FIGURE 10. Strict consensus of 72 most parsimonious trees, derived from color characters deleted from data matrix (Table 2).

vagina; a wide vaginal base; and the uterine duct insertion at a point more distal to the bursa copulatrix. The other characters all relate to color, and it was for this reason that the second analysis, which deleted these characters, was performed. Figure 10 shows that the same tree topology is maintained after deletion of the color characters, although there is less resolution at the terminal branches.

Several apomorphies exhibit no instance of parallelism or reversal. They include: an elongate vagina, a vaginal sphincter, a tubercular vaginal gland, a bipinnate gill, flat gill branchia, an elongate ejaculatory duct, a tubular penis, and a receptaculum seminis that is smaller than the bursa copulatrix.

Further character analysis and testing of the data are needed to strengthen the phylogenetic hypothesis of the genus *Halgerda*.

Cladogenesis

The pattern of species cladogenesis of *Halgerda* is similar to that of other opisthobranch lineages, such as *Thuridilla* (Gosliner 1995). In short, there is little adaptive radiation in the lower branches of the tree and the most derived clades tend to undergo more speciation than lower clades.

Previous studies (Gosliner 1995) have shown that the opisthobranch clades which undergo more adaptive radiation are strictly tropical. *Halgerda* fits this model and they are found only in tropical waters.

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